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Energy intake for maintenance in a mammal with a low basal metabolism, the giant anteater (*Myrmecophaga tridactyla*)

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Energy intake for maintenance in a mammal with a low metabolism, the giant anteater (*Myrmecophaga tridactyla*)

Giant anteaters (Myrmecophaga tridactyla) are among those mammals for which a particularly low metabolism has been reported. In order to verify presumably low requirements for energy, we used 8 captive adult anteaters (2 males, 6 females; aged 1-14 years; body mass between 46-64 kg) in a total of 64 individual experiments, in which a variety of intake levels was achieved on a variety of diets. Digestible energy (DE) intake was quantified by measuring food intake and faecal excretion and analyzing representative samples of gross energy, and animals were weighed regularly. Maintenance DE requirements were calculated by regression analysis for the DE intake that corresponded to no weight change; this resulted in an estimate of 347 kJ DE $kg^{-0.75}d^{-1}$, which is low compared to the 460-580 kJ DE $kg^{-0.75}$ d^{-1} maintenance requirements of domestic dogs. In theory, metabolic requirements below the mammalian average could make species particularly susceptible to overfeeding, if amounts considered adequate for other mammals are given. Anecdotal reports on comparatively fast growth rates and high body masses in captive as compared to free-ranging giant anteaters suggest that feeding regimes in captivity should be further assessed.

Key worlds: anteater, digestible energy, intake, maintenance requirements, body mass

Erhaltungsbedarf für ein Säugetier mit einer niedrigen Stoffwechselrate, der Große Ameisenbär (*Myrmecophaga tridactyla*)

Für den Großen Ameisenbären (*Myrmecophaga tridactyla*) wird eine niedrige Stoffwechselrate berichtet. Um den angenommenen niedrigen Energiebedarf nachzuweisen, führten wir mit 8 in Menschenobhut gehaltenen adulten Ameisenbären (2 Männchen, 6 Weibchen; im Alter von 1-14 Jahren; Gewicht zwischen 46-64 kg) 64 Experimente mit unterschiedlichen Futtermengen und –zusammensetzungen durch. Die Aufnahme an verdaulicher Energie (DE) wurde durch Wiegen des aufgenommenen Futters und der Kotmengen und durch Messung des Energiegehalts repräsentativer Proben bestimmt, und die Tiere wurden regelmäßig gewogen. Der Erhaltungsbedarf errechnete sich durch eine Regressions-Analyse für die Energieaufnahme, bei der es zu keine Gewichtsveränderung kam. Es ergab sich ein Mittelwert von 347 kJ DE $kg^{-0,75}d^{-1}$, welcher im Vergleich zum Erhaltungsbedarf von Hunden (460-580 kJ DE $kg^{-0,75}d^{-1)}$ niedrig ist. Theoretisch macht ein solch niedriger Bedarf eine Art anfälliger für Überfütterung, wenn Mengen gefüttert werden, die für andere Arten adäquat erscheinen. Berichte über schnelleres Wachstum und höheres Körpergewicht von Ameisenbären im Zoo im Vergleich zu frei lebenden Artgenossen legen nahe, dass die Fütterung in Gefangenschaft weiter untersucht werden sollte.

Stichworte: Ameisenbär, Verdauliche Energie, Aufnahme, Erhaltungsbedarf, Körpergewicht

Meinen Eltern

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ESVCN SUPPLEMENT

Energy intake for maintenance in a mammal with a low basal metabolism, the giant anteater (*Myrmecophaga tridactyla*)

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Keywords
giant anteater, anteater, digestible energy, intake, maintenance requirement, body mass

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Summary

Giant anteaters (*Myrmecophaga tridactyla*) are among those mammals for which a particularly low metabolism has been reported. In order to verify presumably low requirements for energy, we used eight anteaters (two males, six females; aged 1–14 years; body mass between 46 and 64 kg) in a total of 64 individual trials, in which a variety of intake levels was achieved on various diets. Digestible energy (DE) intake was quantified by measuring food intake and faecal excretion and analysing representative samples for gross energy, and animals were weighed regularly. Maintenance DE requirements were calculated by regression analysis for the DE intake that corresponded to zero weight change. Differences between individuals were significant. Older anteaters ($n = 3$ animals aged 12–15 years in 29 trials) had lower relative requirements than younger ones ($n = 5$ animals aged 1–7 years in 35 trials); thus, giant anteaters resemble other mammals in which similar age-specific differences in energy requirements are known. However, estimated maintenance requirements were 347 kJ DE/kg$^{0.75}$/day in the anteaters, which is low compared to the 460–580 kJ DE/kg$^{0.75}$/day maintenance requirements of domestic dogs. The lack of knowledge that metabolic requirements are below the mammalian average could make species particularly susceptible to overfeeding, if amounts considered adequate for average mammals were provided. Non-scientific reports on comparatively fast growth rates and high body masses in captive giant anteaters as compared to free-ranging animals suggest that body mass development and feeding regimes in captivity should be further assessed.

Introduction

The basal metabolism of eutherian mammals has been shown to scale allometrically to body mass (BM), usually with an exponent between BM$^{0.67}$ and BM$^{0.75}$ (White and Seymour, 2003; Savage et al., 2004; McNab, 2008). While the exact magnitude of the exponent is the subject of a long-standing scientific debate (Glazier, 2005), the knowledge of allometric scaling as such is crucial for the estimation of energy requirements of animals in practical animal husbandry. For captive nondomestic species, a recommended approach is to estimate basal metabolic rate (BMR) as 293 kJ/kg$^{0.75}$/day, and then estimate maintenance energy requirements (in metabolisable energy, ME) by multiplying the BMR estimate by a factor between 1.5 and 2 (Kirkwood, 1996). For example, when the recommendations for maintenance energy requirements (in ME) for domestic dogs given by Kamphues et al. (2009) are expressed on the basis of $BM^{0.75}$, this corresponds to 1.4–1.8 times 293 kJ ME/$kg^{0.75}$/day. This range covers sedentary and highly active individuals. Assuming that ME constitutes, on average, 91% of digestible energy (DE) in eutherians on meat diets (Robbins, 1993), this translates into estimated maintenance DE requirements of 460–580 kJ DE/$kg^{0.75}$/day for domestic dogs; this value is similar to the 550 kJ DE/$kg^{0.75}$/day given by Kienzle and Rainbird (1991) for domestic dogs. Based on known or estimated dietary contents of DE or ME, recommendations for the amount of food that needs to be fed to an animal can be made (Kirkwood, 1996), and it can be assessed whether given diets are likely to meet or exceed the estimated requirements.

However, mammals vary in their metabolic rate. Many different phylogenetic and ecophysiological factors have been identified that modify mammalian BMR (McNab, 2008); for example, xenarthrans, to which the giant anteaters belong, generally have low metabolic rates. Disregarding these factors, and these deviations from the average, can lead to an over- or underestimation of the energetic requirements of particular species, and also inadvertently to obesity or deficiency (Schwarm et al., 2006). This interspecific variation in energy requirements resembles the intraspecific variation in energy requirements reported between various breeds of domestic dogs (ranging from in 481 to 643 kJ DE/$kg^{0.75}$/day in different breeds for animals aged between 3 and 7 years, Kienzle and Rainbird, 1991).

Among mammals, myrmecophageous or ant- and termite-eating mammals show a distinctive set of anatomical adaptations to their prey that include a reduction of teeth, pointed snouts, large salivary glands and anterior extremities designed for digging (Griffiths, 1968). Anteaters have comparatively low body temperatures (27–33 °C) that fluctuate by 4–6 °C across the day indicating the periodic use of shallow torpor (Wislocki and Enders, 1935; Fernandes and Young, 2008). Accordingly, low metabolic rates as measured by respirometry (Enger, 1957; McNab, 1984; Bosque et al., 1996) and prolonged periods of rest (on average 16.25 h per day, Camilo-Alves and Mourão, 2006) have been recorded in anteaters. Among the potential reasons for the relatively low metabolic rates of myrmecophageous mammals is their mode of food acquisition that usually does not allow them to select very efficiently between prey and detritus (such as soil) (McNab, 1984). Correspondingly, stomach contents or faeces of free-ranging myrmecophages contain indigestible material such as sand, soil or small stones (Bosque et al., 1996; Oyarzun et al., 1996). Note that the presence of soil in anteaters' stomach has also been interpreted as part of a 'gastric mill' (Pernkopf and Lehner, 1937); empirical data for this is, however, lacking. Additionally, larger myrmecophages such as the giant anteater are exception to the general rule that larger carnivores depend on larger-bodied prey (Carbone et al., 1999); most likely, they can only sustain their large body size in their particular nutritional niche by alleviating the energetic constraint of relying on small, dispersed prey through a reduction of their metabolic requirements.

The design of diets for captive anteaters has been discussed repeatedly. Traditional diets consisted of multiple components such as meat, fruits, honey and other ingredients (Meritt, 1976; Widholzer and Voss, 1978; Bartmann, 1983; Derry et al., 1991). The addition of peat to such diets has been found to improve faecal consistency (Brandstätter and Schappert, 2005). In spite of efforts to simplify the diet by using a combination of complete feeds (Edwards and Lewandowski, 1996), such complex mixed diets are continuously being used (Morford and Meyers, 2003a; Osmann, 2004). Most recently, single complete feeds for anteaters have been developed, which are currently increasing in popularity (Steinmetz et al., 2007). While such discussions usually focus on the nutritional composition of the diets under debate, little attention has been paid to the actual amounts that have to be fed. A recent comparison of nutrient and energy digestibilities in carnivorous mammals indicated that for the sake of diet design in zoological collections, the energy content can be estimated with reasonable accuracy using approaches developed for domestic dogs and cats (Clauss et al., 2010a). Thus, matching estimated maintenance energy requirements of anteaters with estimated dietary energy content would be a useful way of assessing the energy provision by an actual feeding regime, if regular weighing is not an option for logistical reasons. As cachectic conditions are a common problem in captive giant anteaters (Morford and Meyers, 2003b), the question of adequate energy supply may be particularly important in this species. Therefore, we performed feeding experiments in which digestible energy intake and body weight changes were monitored on a variety of diets and intake levels, in order to obtain empirical estimates of giant anteaters' digestible energy requirements for maintenance. Experiments were conducted in both winter and summer to test whether season had a measurable influence on the energy expenditure of the animals, expecting higher energy requirements in the wintertime.

Materials and methods

This experiment was conducted at Dortmund Zoo, Germany. Eight adult giant anteaters (two males, six females), between 1 and 15 years old and ranging in body mass from 45 to 63 kg (mean ± SD: 55 ± 5 kg) were used for this study. Animals were kept in their regular indoor quarters at Dortmund Zoo. During the adaptation periods, animals could access outside enclosures in their usual group; during the faecal collection period, all animals were kept individually at all times, and had access to outside enclosures only under supervision. The basic diet consisted of the mix usually fed at Dortmund Zoo (total daily amount for one animal, distributed over two feedings, in g: bananas, 350; apples, 350; pears, 90; tomatoes, 80; boiled eggs without shells, 30; minced beef heart, 350; dry dog food, 190; ground oat flakes, 150; honey, 40; skim curd, 100; *Gammarus pulex*, 9; blended and mixed in 700 ml of water; to this basal mixture 40 g of peat are added per animal and day). The daily food allowance of this mixture was divided into two equal portions fed in the morning and in the afternoon. Water was available for all animals at all times. All animals were weighed every second day during the experimental periods on a mobile scale designed for pigs (ETW 300, Bosche, Damme, Germany).

The individual experimental periods lasted for 2–3 weeks each and always consisted of an adaptation period followed by a 1-week sampling period. During the winter of 2006/2007, eight different treatments were investigated. In the first four periods, the daily amount of this basal mix fed (as fed per animal) varied from 1400, 1600 and 2000 to 2200 g. In the second four periods, various amounts of peat (between 20 and 30 g per animal in addition to the usual 40 g), shrimp meal (between 10 and 30 g per animal) and lucerne meal (between 53 and 93 g per animal) were added to 2000 g of the basal mix, depending on the acceptance of the addition, which varied between individuals; the last diet used consisted of 257 g as fed (per animal and day) of a complete feed designed for insectivores (Nutrazu® Insectivore diet, Brogaarden Zoo Foder, Gentofte, Denmark) mixed in 1 l of water. These additional diets were tested as part of another study in which differences in acceptance and influence on faecal consistency were investigated. In summer 2007, the basal mix was again given in daily amounts of 1400, 2000 and 2200 g as fed per animal. Because of individual feeding preferences, not all animals were included in each experimental period (see Table 1). In total, data for 64 individual trials were obtained.

Table 1 Giant anteaters used in this study, body mass at the beginning and end of the whole experimental period, and the code of the feeding trials in which each individual was used

Animal	Sex	Age* (years)	Body mass (kg) Initial	Body mass (kg) Final	Feeding trial no.†
1	M	6–7	58.8	53.6	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11
2	M	12–13	47.2	46.5	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11
3	F	1	46.0	50.2	5, 6, 7, 8, 9, 10, 11
4	F	2–3	58.4	55.7	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11
5	F	5	55.6	53.7	1, 3
6	F	6	57.2	57.7	1, 2, 3, 4
7	F	12–13	60.3	55.5	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
8	F	14–15	60.8	64.4	1, 2, 3, 4, 5, 6, 7, 8

*Animals used in both summer and winter trials have an age range of two years.
†For the code of feeding trials, see Table 2.

During the sampling weeks of each experimental period, food intake and faecal excretion was recorded by weighing; offered rations were always consumed completely. Defecation frequency was one or two defecations per day. Representative samples of the diets and all excreta were stored frozen at −20 °C until analysis. Dry matter (DM) concentration of feeds and faeces was determined by drying at 103 °C to constant weight. Gross energy (GE) was determined in feeds and faeces by bomb calorimetry (IKA-Kalorimeter C7000, Ika, Stauffen, Germany). All samples were analysed in duplicate.

Intake and excretion of GE were calculated by multiplying the respective amounts of DM with the GE content of the respective sample. The apparent digestibility of GE (%) was calculated as (intake - excretion) × 100/intake, and the intake of digestible energy (DE) was computed as the corresponding fraction of the GE intake. DE intake was expressed on a metabolic body weight basis (kJ/kg$^{0.75}$/day). To estimate maintenance DE requirements across the individuals studied here, we followed procedures outlined by Robbins (1993) and Wolf et al. (2007): linear regression analysis was performed with the DE intake (per kg$^{0.75}$ of the average body mass during the experimental period) as the independent variable and the proportionate body mass change (in % of the initial body mass of the experimental period) as the dependent variable. The x-value at which $y = 0$

then denotes maintenance DE requirements. To analyse the influence of additional factors on maintenance requirements, not only DE intake, but additionally body mass, sex, age (as a continuous variable), and season were included in a step down General Linear Model approach, in which factors that were not significantly different were excluded from the next model. Because age and sex were factors for which not enough different individuals were tested, the effect of repeated measurements could not be included in this evaluation. In order to test for such an effect, we added a General Linear Model in which 'individual' was added as a factor. Statistical analyses were performed with PASW 18.0 (SPSS, Chicago, IL, USA). The significance level was set to $\alpha < 0.05$.

Results

Across all experimental periods, the maximum body mass changes observed were ±0.2 kg per day. Intake and excretion of DM as well as DE intake were 18 ± 4 (range: 10–26) g/kg$^{0.75}$/day, 5 ± 2 (range: 2–10) g/kg$^{0.75}$/day and 315 ± 76 (range: 175–466) kJ/kg$^{0.75}$/day, respectively. The apparent digestibility of GE averaged at 82 ± 5 (68–92)%. Average data for the different feeding experiments are given in Table 2.

In the step down procedure, body mass and season were eliminated as covariates/cofactors from the General Linear Model. In the resulting model ($F_{3,60} = 9.164$, $p < 0.001$, adjusted $r^2 = 0.280$), DE intake ($F_{1,60} = 27.023$, $p < 0.001$), sex ($F_{1,60} = 7.043$, $p = 0.010$) and age ($F_{1,60} = 5.841$, $p = 0.019$) were significant. When repeating the General Linear Model without sex and age, but with the individual animal as a random factor, the resulting model ($F_{8,55} = 6.631$, $p < 0.001$, adjusted $r^2 = 0.417$) again had DE intake ($F_{1,55} = 46.513$, $p < 0.001$) and also individual ($F_{7,55} = 4.437$, $p = 0.001$) as significant covariable/cofactor. The linear regression equations obtained when including all measurements, only males, only females, and animals aged 1–7 years vs. those aged 12–15 years are given in Table 3. Equations indicated an overall average maintenance DE of 347 kJ/kg$^{0.75}$/day (Fig. 1a), a higher maintenance

Table 2 Feeding trials with giant anteaters performed in this study in winter/summer, at various levels of dry matter intake (DMI in g/kg$^{0.75}$/day), dietary gross energy content (GE in MJ kg/DM), apparent digestibility (aD) of GE (in %), and the body mass (BM) change (in % of the initial BM at the start of the respective feeding trial). Data are averages ± standard deviation across all individuals

Feeding trial no.	Diet	Season	*n total*; males/females; young/old*	DMI	GE	aD GE	BM change
1	Zoo diet†	Winter	7; 2/5; 4/3	18 ± 2	21.7	82 ± 4	−0.04 ± 0.08
2	Zoo diet	Winter	6; 2/4; 3/3	17 ± 2	21.4	83 ± 8	−0.09 ± 0.07
3	Zoo diet	Winter	7; 2/5; 4/3	13 ± 1	21.3	81 ± 3	−0.17 ± 0.06
4	Zoo diet	Winter	7; 2/5; 4/3	21 ± 5	21.4	84 ± 3	0.09 ± 0.09
5	Zoo diet	Summer	6; 2/4; 3/3	20 ± 3	21.5	86 ± 4	0.03 ± 0.11
6	Zoo diet	Summer	6; 2/4; 3/3	14 ± 1	21.9	80 ± 7	−0.27 ± 0.07
7	Zoo diet	Summer	6; 2/4; 3/3	19 ± 3	21.5	82 ± 5	0.05 ± 0.16
8	Zoo diet + peat	Winter	6; 2/4; 3/3	19 ± 2	21.7	77 ± 5	0.00 ± 0.11
9	Zoo diet + shrimp meal	Winter	5; 2/3; 3/2	17 ± 5	21.8	85 ± 3	−0.20 ± 0.12
10	Zoo diet + lucerne meal	Winter	5; 2/3; 3/2	22 ± 4	18.9	80 ± 2	0.03 ± 0.18
11	Complete feed‡	Winter	4; 2/2; 3/1	19 ± 5	22.1	81 ± 7	−0.04 ± 0.15

*Young = aged 1–7 years, old = aged 12–15 years.
†See *Methods* for the composition of the regular zoo diet.
‡Nutrazu® Insectivore diet, Brogaarden Zoo Foder, Gentofte, Denmark.

Table 3 Results of linear regression analysis: weight change (% starting weight) = *a* × digestible energy intake (in kJ/kg$^{0.75}$/day) + *b* in giant anteaters for in the whole dataset and in different subsets

Data	*n* (trials/individuals)	*a*	*b* (95% CI)	r^2	p
All measurements	64/8	0.001	−0.347 (−0.497, −0.198)	0.20	<0.001
Males	22/2	0.001	−0.564 (−0.915, −0.213)	0.32	0.006
Females	42/6	0.001	−0.341 (−0.519, −0.163)	0.22	0.002
1–7 years	35/5	0.001	−0.437 (−0.662, −0.211)	0.26	0.002
12–15 years	29/3	0.001	−0.301 (−0.511, −0.091)	0.20	0.015

Note that in a General Linear Model, the effect of sex and age was significant (see *Results*).

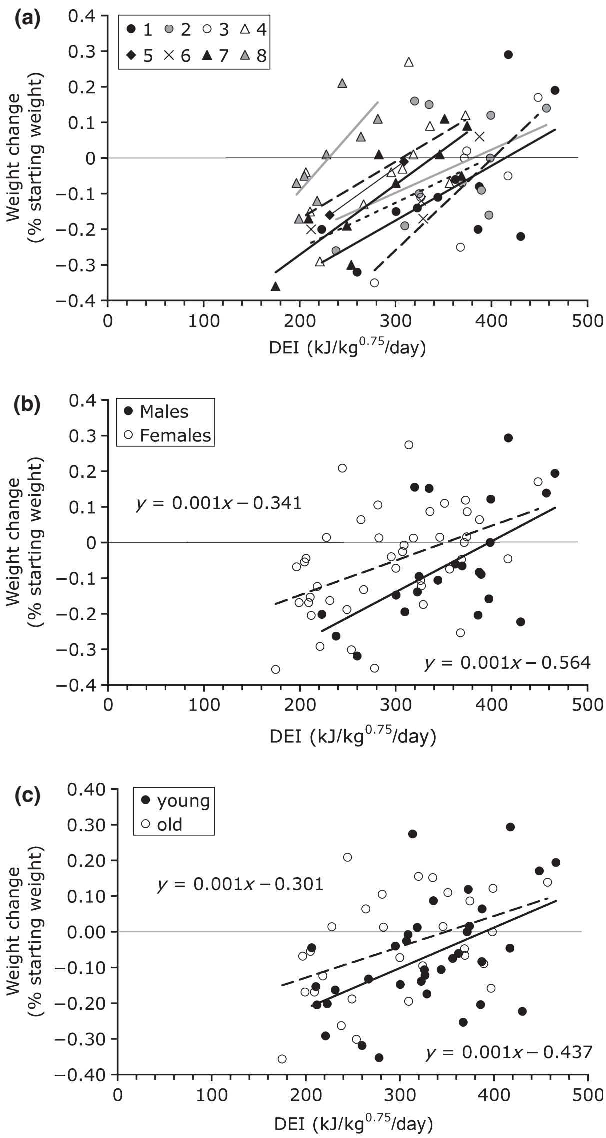

Fig. 1 Relationship of weight change and digestible energy intake (DEI) evaluated from a series of 64 trials performed in winter and summer with 8 giant anteaters (*Myrmecophaga tridactyla*; two males, six females) of various ages. (a) Regression for individual animals; the effect of individual was significant (regression lines for animal 1 [11 trials] – lower thick black line; 2 [11 trials] – lower grey line; 3 [7 trials] – lower interrupted line; 4 [11 trials] – upper interrupted line; 5 [2 trials] – thin black line; 6 [4 trials] – dotted line; 7 [10 trials] – upper black line; 8 [8 trials] – upper grey line); (b) regressions for males ($n = 2$ in 22 trials) and females ($n = 6$ in 42 trials; interrupted line); c) regressions for animals of 1–7 years of age ($n = 5$ in 35 trials) and of 12–15 years of age ($n = 3$ in 29 trials; interrupted line).

requirement in the two males of this study compared to the five females (Fig. 1b), and a higher maintenance requirement in the younger as compared to the older animals (Fig. 1c).

Discussion

The results of this study support previous findings that giant anteaters have a comparatively low metabolism amongst eutherian mammals. With 347 kJ DE/kg$^{0.75}$/day, the estimated maintenance DE requirement is much lower than the 460–580 kJ DE/kg$^{0.75}$/day found in dogs and other mammals (see *Introduction*). Large as this difference is, it should be noted, however, that the anteaters' requirement represents 60–75% of the 'average' mammal range of DE; therefore, it might not be as low as the 34% of the 'average' mammal range reported for basal metabolic rate measurements by McNab (1984).

The presence of a significant effect of age on maintenance energy requirements demonstrated in these anteaters is consistent with findings in domestic dogs (Kienzle and Rainbird, 1991; Burger, 1994; Finke, 1994; Harper, 1998). The reduction in maintenance requirements with age is usually associated with a lower degree of activity in older individuals. In contrast to findings in dogs where gender did not influence maintenance energy requirements (Kienzle and Rainbird, 1991), the two males of our study had higher requirements than the five females (165% of the female requirement). We can only speculate that these males were more active than the females. Increased activity in male giant anteaters might be caused by the reported reduced tolerance of same-sex neighbours in males, including an increased frequency of agonistic encounters (Shaw et al., 1987). Under captive conditions, even if animals are kept individually, the typically close proximity of enclosures of conspecifics might result in subtly increased levels of agitation (Clauss et al., 2010b) and hence higher energy expenditure. Additionally, the continuous presence of a relatively large group of females (six to eight animals), most of which are in regular oestrus cycle (Schauerte, 2005), will be a cause of frequent agitation for the males. However, given the fact that 'individual' was a significant factor when evaluating maintenance requirements statistically, we cannot exclude that observed differences between sexes and age groups are an artefact due to our low number of individuals investigated, and these results should therefore considered with caution.

In contrast to our expectations, there were no significant differences in maintenance energy requirements between the summer and the winter trials. We can only speculate that this indicates that the housing of the animals at this zoo protected them from any cold stress that might have occurred during the winter period.

Below-average metabolic requirements incur the risk of intuitive overfeeding. It remains to be demonstrated whether the low relative metabolic requirements of giant anteaters actually do lead to such problems. Though scarce, there is some tentative evidence for an effect of a high energy supply in captivity. For example, Shaw et al. (1987) compared the growth rate of a captive and a free-ranging giant anteater, and speculated that the higher growth rate in the captive specimen might be a result of both intensive feeding and reduced exercise. Additionally, the body masses recorded for free-ranging adult giant anteaters usually do not surpass 40 kg (Shaw et al., 1987; Medri and Mourão, 2005), whereas most adult specimens in captivity (including the individuals used in this study) surpass this threshold and reach body masses of up to 70 kg (Morford and Meyers, 2003b). To date, it is unknown whether such animals are truly obese, or if they just show increased growth, and whether body condition has relevance for their survival or husbandry success. Future studies should address the question whether offering food in amounts that meet, but do not exceed the species' maintenance requirements, leads to less heavy specimens. However, any husbandry measures that include diet manipulation should ideally not only follow fixed recommendations, but adjust amounts fed in response to regular weight measurements.

Traditionally, considerations on feeding exotic animals often focus on ingredient choice and diet composition, but disregard the actual amounts offered (e.g. Morford and Meyers, 2003a). The deviation of the maintenance energy requirement of giant anteaters from the general eutherian average demonstrates that the amount fed, and therefore the amount of energy provided to these animals, deserves particular attention in the future.

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